LABORATORY BULLETIN NO. 13
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The Development of Nestling Feathers

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I. INTRODUCTION.

The purpose of this paper is to give a more complete account of the development of the down, or Neossoptile, than has been given by previous writers and to show the true relation of this structure to the first definitive feather.

"The first clothing of the newly hatched bird consists of more or fewer soft feathers, on the whole resembling the Downs of adult birds, but possessing several characters which make it advisable to distinguish them, by the name of 'Neossoptiles,' from those feathers which subsequently appear, and may be called 'Teleoptiles,' the former being as it were the first generation to which others follow in constant succession, so long as the bird lives.

"Neossoptiles are characterized by (1) a very short calamus, (2) an insignificant or ill-defined rachis—if there be one at all, (3) the almost universal absence of cilia (barbules), (4) long and slender rami (barbs), (5) absence of aftershaft, except in Dromæus. To the combination of these characters is due the soft or downy structure of these feathers.

"Teleoptiles, whether Contour-feathers or Downs, are each originally preceded by a Neossoptile, the base of which is in direct continuity with the tips of the rami of its succeeding final feather, but, owing to a shortened process of development of cœnogenetic conditions, many, or even all Neossoptiles may occasionally be suppressed, so that the tips of the first feathers to appear are actually those of the second generation." (A Dictionary of Birds, A. Newton, p. 243.)

Though a continuity between the nestling down ("Neossoptile") and the nestling definitive feather ("Teleoptile") has been recognized, the former has been regarded as a relatively complete and distinct feather. I shall attempt to show that the "Neossoptile" is only a more or less differentiated distal part of the first "Teleoptile."

My attention was attracted to this relationship while studying the terns (*Sterna hirundo, S. dougalli, and S. antillarum*), and the gulls (*Larus atricilla*) which bred abundantly in the vicinity of Woods Holl, Mass., during the summer of 1903. Further study of these birds at all ages, and of numerous specimens of various species of birds, led to an examination of the evidence for the accepted views.

Under the stimulus of Professor C. O. Whitman's interest and encouragement the task of gathering the requisite material was carried forward. It would have been difficult to carry on the necessary field studies and secure the material from the terns and gulls but for the aid rendered by Dr. F. B.

Sumner, Director of the U. S. Fish Commission. To Capt. Vinal N. Edwards, of the Fish Commission, I am indebted for many valuable hints and advice relating to the habits of these birds; and to Dr. R. M. Strong, for valuable suggestions and advice.

II. MATERIAL.

Material for histological and cytological study was obtained from the following birds: *Sterna hirundo, S. dougalli, Larus atricilla, and Merula migratoria.* Developing feathers were also secured from the chick and domestic duck, incubated both artificially and naturally. Dry feathers with downs attached for grosser study came from the following sources: Mr. H. C. Oberholser, under the direction of Dr. T. S. Palmer, from the U. S. National Museum collections; Mr. Frank M. Chapman, from the American Museum of Natural History; Messrs. C. C. Adams and N. A. Wood, from the collections of the University of Michigan; Prof. E. L. Moseley, from his private collection of American and Philippine birds; Dr. N. Dearborn contributed both alcoholic and dry material from the Field Columbian Museum; and Dr. C. O. Whitman, fresh material from his pigeons. To all of these gentlemen I wish to express my thanks. The collections of Oberlin College furnished some material not obtainable elsewhere.

III. METHODS.

The following fixing fluids were used for chicks from five to twenty days' incubation: (1) Kleinenberg's picro-sulphuric mixture, (2) saturated aqueous solution of corrosive sublimate, (3) Hermann's fluid, (4) alcohol-formaldehyde mixture (70% alcohol 98 parts, 40% formaldehyde 2 parts). After proper fixation, pieces of skin containing the desired structures were cut away and later treated as ordinary histological tissues.

For the latest stages, Hermann's fluid was found somewhat superior, but for the earlier stages the alcohol-formalin mixture gave the most satisfactory results. Since most of the material must be put into the killing and fixing fluids on the collecting grounds to insure a normal condition of the cellular structure, the latter reagent was the only one found practicable, because the tissues could remain in it indefinitely without material injury, while more than five hours in the others proved fatal to good results. It was usually necessary to remain in the field for an entire day, because the nearest collecting ground was five miles away by water. Furthermore, after the alcohol-formalin fixation the tissues stain equally well in any of the stains used, even the iron hæmatoxylin. For the earlier stages, the Hermann's fluid did not give good fixation, and it was always likely to blacken the tissues unequally and unduly. The picrosulphuric was very difficult to handle because it required a great length of time for washing out before stains could act; even after two weeks of careful washing, staining was usu-

ally difficult and unsatisfactory. The corrosive sublimate had a strong tendency to make the tissues brittle.

With the alcohol-formalin solution, a fixation of six hours was always sufficient, and four hours would often suffice. Washing out of the formaldehyde was effected by the use of 70% alcohol, changing about ten times. Various combinations of alcohol and formaldehyde were used, but the formula given proved the most satisfactory.

The only satisfactory method for clearing and infiltration with paraffin was the chloroform method. Tissues were first cleared in chloroform and then placed in a saturated solution of paraffin in chloroform two to five days, according to the thickness of the tissue. They were then transferred to melted paraffin for six to ten hours, and imbedded in hard paraffin (melting at 52° C).

Serial sections were cut one to ten *micra* thick, mostly three *micra*. Complete series of all but the latest stages were easily obtained. For the thinnest sections, a temperature between 55° and 60° F., while cutting, was found necessary, and the best results were always obtained at temperatures not much above 60°.

For affixing sections to the slide a combination of the Mayer's albumen fixative with the water method was found the most satisfactory, but many times, particularly with the larger specimens, the albumen fixative was unnecessary. With the latest stages, where many elements were cornified, it was necessary to paint the dry slides, bearing sections, with a film of very thin celloidin solution to insure the retention of the sections during subsequent processes. These cellodin films were sometimes detached from the slide for quicker and more accurate staining.

Various stains were used, the two giving the most certain and satisfactory results being Delafield's hæmatoxylin and the Heidenhain iron hæmatoxylin. Delafield's hæmatoxylin was used very dilute in distilled water—a pipette full of the stain to about 150cc of distilled water, the exact proportions being unimportant. Slides left in this weak stain for 48 hours were always overstained, and reduction of the stain was accomplished by the use of weak acid alcohol. A saturated solution of eosin in 95% alcohol was used in the process of dehydration for double staining, to bring out the cornifying elements.

Feather germs were sectioned longitudinally, transversely and obliquely for all stages, and the sections were mounted in Canada balsam. A great deal of material was also teased on the slide and mounted in glycerine temporarily for immediate study. It was usually necessary to stain such material before teasing so that the structures could be seen. Dry nestling feathers with downy tips were dehydrated and cleared, and then mounted whole in Canada balsam for study of the entire feather.

For the earlier stages of the definitive feather it was necessary to cut out pieces of the skin containing the desired material. All attempts to pull

feather germs out by means of the down were ineffectual. Likewise, barb-vanes pulled out were useless for any other study than that of the complete down, the proximal portion invariably being torn.

Plate V represents down attached to definitive feathers photographed enlarged. Plates VI, VII, and VIII were made by direct printing upon sensitive paper. In the latter case the feathers were placed upon a plate of clear glass, and a sheet of sensitive paper was pressed down upon them with the sensitive face against the feathers. The whole preparation was then exposed to the light in the regular printing out photographic process. Developing papers were used, but these gave less satisfactory results. Of course the prints thus obtained give very little or no color patterns. The feathers act as opaque objects upon the sensitive paper. This method served admirably where the photographic method must fail because the color contrasts between the down and the definitive feather make any sort of a background act as a neutralizing agent for one or the other. Dividing the background to suit the two contrasting elements spoils the picture.

In the further discussion of this subject it will often be necessary to speak of the barbs and barbules collectively, and for this purpose I shall employ the term barb-vane. The feather-vane is made up of a median shaft with barbs attached on each side. The barb is the median axis of what I call a barb-vane, and the barbules are arranged on the barb as the barbs are situated on the shaft. Likewise, during the earlier developmental stages of the down, before barb and barbule elements are clearly defined, the ridge from which these structures are to result will be called barb-vane ridge.

IV. THE DEVELOPMENT OF THE NESTLING DOWN.

A. *The Feather Germ.*

Davies (1889) seems to be the last investigator to study the developmental stages of the nestling down. His is by far the most thorough and the most accurate treatment of the subject, but he gave no attention to the development of the barbs and barbules. He gave an extended review of the literature up to the time of his work, pointing out the contribution which each successive author made to the subject.

According to Davies (p. 571), the down first appears in the pigeon embryo on the fifth day of incubation as round white spots in the two-layered skin. These two layers he terms "epitrichial," outer (Pl. I, Fig. 6, Ep) and "mucous," inner (Pl. I, Fig. 6, Mp). These white spots are produced by groups of dermal cells (Drm. pp) closely pressed against the epidermis, and cause slight prominences upon the skin surface. Division of the mucous cells which lie over these groups of dermal cells now begins longitudinally, causing an arching of the epidermis, and the cavity in the skin thus formed becomes filled with dermal cells which are also rapidly dividing (Pl. I, Fig. 6). At this time the epitrichial cells undergo transverse divis-

ion, and this layer remains single. The dividing mucous cells, on the contrary, rapidly form two or more layers, or a confused mass of cells bounded by a well marked layer next to the derma (Pl. I, Fig. 7).

In the further growth of the down papilla the cells on the anterior surface divide more rapidly than those on the posterior surface, so that the whole papilla is turned sharply backward (Pl. I, Fig. 1), finally coming to lie almost parallel to the skin surface. No sooner has this papilla taken a definite turn backward than cell division within it ceases except in a narrow region at its base just outside the skin surface; consequently all further growth of the papilla results from this narrow region of division and from the growth of the individual cells which are supplied with nutriment by numerous blood capillaries in the pulp.

As long as the down papilla continues to elongate it continues to be an evagination of the epidermis with a core of dermal tissue. When the papilla has attained its full length, save for some further growth of its individual cells, the continued cell division results in an invagination of the mucous layer of the feather-germ at an angle of about 160° with the down papilla. At first this invagination is pushed farther in by the division of the cells at the skin surface, but the cell division soon changes its position to the proximal end of the invagination, and henceforth all growth proceeds from this proximal end by cell division there. This invagination is the beginning of the definitive feather (Pl. I, Fig. 1, grm. df). The epitrichial layer does not participate in this invagination, and therefore does not contribute to the structure of the definitive feather.

My investigations have shown that the invagination of the feather germ, which represents the beginning of the definitive feather, begins about the 12th day of incubation of the chick, of the duck, of the terns, and of the robin. My observations also indicate that with these birds differentiation of the definitive feather elements proceeds slowly until about the 17th day, after which time the definitive feathers develop rapidly. During the interval between the 12th and 17th days the feather rudiment seems to be engaged chiefly in the formation of the feather follicle.

At the base of the down we may distinguish three sorts of cells, following Davies' classification. The epitrichial cells, consisting of a single outer layer (Pl. I, Fig. 6, Ep), an inner layer of mucous cells cubical in form and more or less regular (Pl. I, Fig. 6, cl. cyl), and a mass of more or less irregular cells between these two layers (Pl. I, Fig. 6, cl. im). The innermost layer may be distinguished as the "cylinder cell layer" (cl. cyl), and the irregular cells as the "intermediate cells" (cl. im). These two layers are derived from the mucous cells by division.

I can add little to Davies' account of the early stages in the development of the down. I submit Figures 1, 6, 7, 8, and 9, as amplifications of those given by him. His work was mostly done upon pigeon and canary embryos, while these figures are from a chick embryo. I have also studied

tern, gull, and duck embryos, all of which showed essentially the same characteristics represented by these figures.

B. *The Barbs and Barbules.*

Differentiation of the epidermal wall of the nestling down begins as soon as the down papilla has passed distally beyond the region of cell division. It therefore follows that the distal end of the down papilla is more developed than any region proximal to it. Cross sections at different distances from the distal end will therefore give different stages in the development of the down structures.

At the level (7, Fig. 1, Pl. I) where cell division has just been completed one finds the condition represented by Figure 7, Plate I. The dermal nuclei are numerous and lie closely pressed against the layer of cylinder cells (cl. cyl), being separated from it by a basal membrane (mb. ba). A layer of cubical intermediate cells (cl. in) rests upon the cylinder cells, but peripheral to this layer the intermediate cells have become elongated and irregular, becoming the sheath cells (cl. tu).

Figure 8 illustrates the condition at the level 8 in figure 1, where the basal membrane has pushed in dividing cylinder cells and intermediate cells into groups. Figure 9 shows the barb-vane ridges completely separated from each other except at their extreme base. The cylinder cells are much flattened and elongated and their nuclei are far apart. The intermediate cells are definitely arranged into three groups—a central row of cells indicate the position of the so-called axial plate (ax. pl) and on each side of this plate a series of barbule cells (bbl. cl).

It will be at once evident that the differentiation of the down barbs and barbules is so similar to the differentiation of the same structures so fully described by Strong (1902) for the definitive feather that to follow the steps of differentiation farther would be only to duplicate what has already been done. Some minor differences should be mentioned.

1. The down rudiment has a much shorter diameter and fewer ridges than the definitive feather. Figure 4, Plate I, represents a semidiagrammatic cross section at about the middle of a down from the Common Tern (*Sterna hirundo*), and Figure 5, a similar cross section of a definitive feather from the same species. The down has a sort of radial symmetry, the ridges being approximately equal in size, while the definitive feather has a decided bilateral symmetry due to the shaft rudiment X and the wedge-shaped piece opposite the shaft rudiment where the two vanes will separate when the sheath falls away.

2. The down barbules are never provided with hooked barbicels (Fig. 52, Pl. IV), hence the down has a loose, light texture, in contrast to the firm texture of most definitive feathers. Although hooked barbicels are wanting in the down, several of the distal barbule cells send out one or two filamentous prolongations from their distal ends (Figs. 52, 55, Pl. IV) which resemble the unhooked barbicels of the definitive feather barbules (Fig. 54, Pl.

IV), and are undoubtedly homologous structures. The barbules of all plumulaceous feathers, and the plumulaceous proximal parts of most other definitive feathers lack hooked barbicels.

3. Klee (p. 12) speaks of two chief ridges (*Hauptstrahlen*) in both the down and the definitive feather, which mark the place where the shaft will be developed. A few millimeters proximal to the distal end of the definitive feather such chief ridges make their appearance, but I have been unable to find anything corresponding to them in any down.

4. In most descriptions of the down the statement is made that barbules are sometimes wanting upon the barbs. I have been unable to find any case in which this is true for the whole down except in the spike-like first feathers of the cuckoos.

In the definitive feather the barb-vane ridges develop in succession proximally along the course of the feather, and each ridge occupies but a fraction of the whole length of the feather. In the down, on the contrary, each barb-vane ridge is continuous through the whole length of the down, and usually passes without interruption into the definitive feather barb (Pl. I, Fig. 2, Pl. IV, Figs. 139, 141, 142, Pls. V, VI, VII, VIII, Figs. 56 to 138). Upon this point I find myself in disagreement with Davies, who states (581): "Es muss daran erinnert werden, dass die Längsleisten, sobald sie sich in den Federkeimgrund erstrecken, an Umfang abnehmen. Die Grenze, bis zu welcher diese Verkleinerung stattfinden kann, ist grossem Wechsel unterworfen; jedoch in dem Falle, welchen wir als typisch betrachten können, verschwinden die Leisten vollkommen; und wenn die Verhornung diesen basalen Theil des Federkeimes erreicht, dann wird ein kurtzer horniger Cylinder gebildet, welcher mit dem Grunde der Strahlen in Zusammenhang steht. Dieses cylindrische Gebilde ist die sogenannte Spule." While Davies regarded the formation of a "quill" in the first down as the typical condition, he noted some variations, as further quotations will prove.

"Solch eine typische Dunenspule ist jedoch bei der Taube nicht sehr häufig. Gewöhnlich verschwinden die Leisten nicht vollkommen, obgleich sie eine bedeutende Verminderung ihrer Grösse erfahren" (p. 581).

"In der Gegend der Dunenspule nimmt der Process der Leistenbildung in einem grösseren oder geringeren Grad ab, oder kann sogar gänzlich aufhören aber sobald wir die Spitze des definitiven Federkeims erreichen, finden wir ihn noch einmal in vollem Gange."

"Zuweilen gehen die Leisten, welche oben die Dunenstrahlen hervorgehen liessen, nach unten direkt in diejenigen Leisten über, welche die obersten der definitive Federstrahlen oder Aste bilden. Wenn wir bei einer in Entwicklung begriffenen Schwungfeder, welche gerade die Dune aus der Haut in die Höhe hebt, die Hornscheide abkratzen, welche die Wurzeln der Dunenstrahlen zusammenhält und damit den oberen Theil der definitiven Federscheide, dann sehen wir gewöhnlich, dass hier und da zwei oder drei Dunenstrahlen an ihren Wurzeln verschmolzen sind und dass dieser verschmolzene theil wieder in eine grössere als die Zahl der Dunenstrahlen beträgt,

welche ihn bildeten. Auch findet man leicht einen einzelnen Dunenstrahl, welcher sich in zwei definitive Federäste theilt. Sogar bei vollkommener Verschmelzung der Dunenstrahlen und Bildung einer typischen Spule kann man oft sehen, dass diese sich an ihrem tieferen Ende in vier oder fünf grosse Theile auflöst, welche erst allmählich sich zertheilen, um die definitive Federäste zu bilden. Wir können thatsächlich jeden Ubergang wahrnehmen zwischen der typischen cylindrischen Dunenspule und der direkten Fortsetzung der Dunenstrahlen in eine gleiche Anzahl von definitiven Federästen" (586-7).

V. THE RELATION OF THE DOWN TO THE FIRST DEFINITIVE FEATHER.

Klee (1886) and Davies (1889) announced that the first definitive feather is produced by an ingrowth of the base of the down papilla, with the cornification of the proximal end of the down. In other words, the first down and its succeeding first definitive feather develop from the same cutis papilla.

Klee (p. 39) holds that the shaft of the definitive feather is continuous with the shaft of the down "feather," which is clearly an error, as I shall show. Davies (quotation antea 7 and 8) regarded the nestling down as a structure typically complete in itself, possessing a quill and sometimes a shaft, and he considered the lack of a quill as an exceptional condition. I shall attempt to show that a shaft and a true quill are never formed, but that there is always a direct continuity between the barb-vanes of the down and those of the first definitive feather.

There seems to be no detailed account of the manner in which the barb-vanes of the down pass into the barb-vanes of the first definitive feather. I shall therefore discuss this point at some length.

Figures 140, 141, and 142, Plate IV, illustrate three conditions of the barb-vanes after complete cornification, in the region connecting nestling down with first definitive feathers. In Figure 140 the barb-vanes are united into a tube surrounding the pulp cavity. In Figure 141 the barb-vane has no connection with any other barb-vane. It divides into three definitive feather barb-vanes. In Figure 142 the same condition is seen, but barbules are present along the whole course of the barb-vane.

Figure 140 represents the condition where a horny cylinder is formed at the proximal end of the down into which the down barb-vanes disappear proximally and out of which the definitive feather barb-vanes emerge. This horny cylinder is the so-called "quill" of the down. I have found this to be a rare condition in all birds except the Picarian and Passerine birds, where it is more often found than elsewhere (Pl. VIII, Figs, 124 to 136, and 138).

The condition represented by Figure 141 is a common one. Barbules are often lacking for a short distance—usually less than a millimeter—distal to the branching of the barb-vane into the definitive feather barb-vanes, when branching occurs; but barbules are often indicated by irregularities upon the

surface, or even by slight projections from the surface, representing rudimentary barbules, as in this figure.

Figure 142 represents a common condition found among all of the water birds except the Anseriformes. This is undoubtedly the typical condition, as I hope to demonstrate in the following detailed discussion of the developmental processes which take place in the region of transition from nestling down into first definitive feather.

Before discussing the development of the feather in the region which is supposed to lie between the down and the definitive feather, I will sketch in a general way the passage of a first down barb-vane into the definitive feather barb-vane or vanes. Figures 10 to 46, Plates II and III, have been prepared to illustrate the three conditions represented by Figures 140, 141, and 142.

Proceeding from the down at the level 10, Figure 2, Plate I, where the down is complete and only waits the loss of the sheath to expand, we will follow first the process which results in the condition illustrated by Figure 141, Plate IV, as shown in Figures 10 to 20, Plate II.

In Figure 10, Plate II, two down barbs are shown in cross section with their barbules cut at different distances from their attachment to the barbs. Cellular structure has been entirely obliterated by the cornification of the cells. Figures 10 to 20 were taken at intervals of nearly 36 microns proximally toward the distal end of the definitive feather. Barbules rapidly disappear and none are formed in the region of transition. The last vestige of a barbule will therefore be its base where it is attached to the barb. The medulla of the barb disappears and the shape of the barb in cross section becomes somewhat circular.

In Figure 12, remnants of nuclei begin to indicate the cellular origin of the barbs, and in 14 scattered cells are found in one side of the barb. In 15 the cells predominate, and in 16 cornification has entirely disappeared. The larger barb becomes irregular, in 17 there is an evident division in progress, which is completed in 18. In 19 the three cellular masses begin to assume the character of barb-vanes, and in 20 they are unmistakably barb-vanes with cylinder cells, barbule cells, and axial plate. One of the down barbs has remained single and has passed directly into one definitive feather barb, while the other has divided and merged into two definitive feather barbs.

Figues 21 to 28 illustrate the passage of a down barb from a 21-day chick embryo into two definitive feather barbs, after complete cornification of all cells. No barbules are shown.

Figures 29 to 39, Plate III, were taken from a 21-day chick embryo ready to hatch, at somewhat irregular intervals, from the region marked 29 to 39 in Figure 3, Plate I. Figures 29 to 33 are entire cross sections of the down. In Figure 29 seven down barbs are seen in cross section (brb), and two masses of cornified material (hr) which are the fused proximal ends of the several remaining down barbs. Figures 30, 31, 32, and 33 illustrate the further fusion of the proximal ends of the barbs into cornified material (hr)

until all trace of individual barbs is lost (33). Passing proximally along the feather, Figure 34 shows this cornified material again dividing into somewhat irregular but elongated masses. Figure 35 shows these masses becoming more regular in form and arrangement; Figure 36 shows them assuming the form of a cornified barb with outlines of barbules appearing; and Figures 37, 38, and 39 show them as definite definitive feather barb-vanes, Figure 37 well toward complete cornification of the elements, and Figure 39 much less cornified because this figure was taken from the pulpy tip of the definitive feather. It should be borne in mind that Figures 29 to 39 are rather oblique than exact cross sections, nearly in the line X in Figure 3, Plate I. All exact cross sections through the region of transition would show a broken cornified ring (Fig. 29, hr), because, as I have already indicated, the plane of growth is always oblique, as pointed out by Davies and Strong for the definitive feather. This obliquity is shown in Figure 3, Plate I, in the line X, which corresponds roughly to the angle which the down makes with the skin surface. In a plane parallel to the transverse axis of the down, the posterior surface is less developed. The cells here were retarded in their division while the papilla was turning backward, whereas a more rapid division of the cells took place on the anterior surface.

Figures 10 to 20, Plate II, prove that at the time when the barb vane ridges are beginning to be differentiated as such at the distal end of the definitive feather, practically all of the barb-vane elements at the proximal end of the down have become cornified and their cellular nature obliterated. Hence, in order to trace the cytology of the transition from the down barb into the definitive feather barb it became necessary to study feathers at different stages of development. We will first consider the case illustrated in Figure 139, Plate IV, where no barbules are formed at the extreme proximal end of the down just before it branches into definitive feather barbs.

At X in this transition region, at an early stage in development, the epidermal cells are arranged as represented by Figure 7, Plate I. In other words, division of the mucous cells has proceeded in the usual manner—there is no indication that a fully formed feather will not be developed at this point. At a little later stage of development (Fig. 40, Pl. III) barb-vane ridges (brb. crs) are indicated by a more rapid proliferation of the intermediate cells (cl. in) at certain places, where the cells are alike in shape and size, and differ from the surrounding cells. Figure 41 illustrates a still later stage of development, at which a group of similar intermediate cells (brb. crs) has become definitely separated off from those cells which surround it. Figure 42 shows the differentiation further progressed, Figure 43 shows the cornification of the cells begun and the retreat of the barb ridge toward the periphery, and Figure 44 cornification of the barb and almost complete obliteration of cellular structure. The whole epidermal wall is here far toward maturity. It is at once evident that a decreased differentiation of the intermediate cells in this region has resulted in a barb devoid of barbules. The

fact that relatively few of the intermediate cells are involved in the formation of the barb indicates that the residual intermediate cells represent the missing barbules.

The progress of transition which results in a so-called "quill" or tube differs in some important particulars from that just given. In the early stages of development no difference is recognizable, but at a little later stage the whole mass of intermediate cells (Fig. 45, Pl. IV, cl. in) as well as the sheath cells (cl. tu) become much flattened, their nuclei elongated, and their cell boundaries lost in a mass of fibrous tissue. Only the row of cells next to the pulp, representing the cylinder cell layer, retains its characteristic shape. At a still later stage in development, represented by Figure 46, in which the epitrichial sheath is not shown, cornification of the outer rows of cells, representing the region of the sheath cells, has taken place, only suggestions of its original fibrous structure remaining. The outermost intermediate cells have become almost wholly fibrous, narrow spaces representing the position of the nuclei. The process of cornification now proceeds rapidly until practically all of the intermediate cells become cornified, and the cylinder cell layer becomes fibrous. Figure 33, Plate III, represents the final stage in development. That the formation of this horny tube is wholly different from the process by which the shaft and quill of the definitive feather are formed, as described by Davies (p. 594 *et seq.*), is evident. Instead of being a process designed for the accomplishment of a definite work—the building of a shaft and quill—it appears to be due to a lack of differentiation of the cell mass and a short cut to cornification of the tissues induced by a reduced blood supply to this part of the feather during the period when the cells would be showing differentiation if supplied with sufficient nourishment. It is significant that this condition of a cornified ring instead of the normal barb-vanes is more often found among the strictly altrical birds which are hatched in a helpless condition. It is well known that the first few days after the hatching of altricial birds are the most critical days of their lives. During this critical period there appears to be no growth of the down. An American robin which hatched on the fourteenth day of incubation possessed the usual down upon the head and back. These downs made no further growth. It was not until the fourth day after hatching that the skin gave evidence of the beginning of the definitive feathers. On the eighth day after hatching the skin surface was exposed to the drying influences of the air before renewed activity in the feather germ began. During this interval of four days the so-called "quill" was formed at the proximal end of the down by the rapid drying of the imperfectly formed barb-vane ridges.

Although this horny cylinder seems often to be uniform in thickness for its whole circumference, it frequently divides along lines continuous with the barbs of the down, or may be made to so divide by gently rubbing it between two hard surfaces, thus establishing the continuity between the down barbs and the definitive feather barbs.

The material which furnished the basis for Davies' studies of the development of this "quill" was obtained from the canary embryo chiefly. It is a strictly altricial bird.

Figure 142, Plate IV, illustrates the passage of a down barb-vane into three definitive feather barb-vanes where barbules are present along the whole course of the vane. The lengthened barbules of the down become shorter as the distal end of the definitive feather is approached and these shortened barbules gradually assume the typical character of pennaceous feather barbules. Figure 55 is a complete barbule taken at 55 in Figure 142, Plate IV, and Figure 54 is the distal four-fifths of another barbule taken from the region 54, Figure 142. Figure 52, Plate IV, represents a normal down barbule. Since barbules are present along the whole course of a barb of this sort there will be no interruption of the normal development of the barb-vane ridge, and where a down barb is continuous with a single definitive feather barb, instead of with several definitive feather barbs, the only indication of the beginning of the definitive feather barb will be the development of hooked barbicels, provided the definitive feather is pennaceous in character. If the definitive feather is plumulaceous in character no hooked barbicels will be developed. It is common knowledge that the fluffiness of plumulaceous feathers, like ostrich plumes, is due to long and slender barbules without hooks. Pennaceous feathers are provided with shorter and stiffer barbules upon which some hooks are developed.

The first feathers of the Anserine birds are mentioned as illustrating the development of both shaft and quill in the first down. My studies of the duck embryo prove that the first feathers begin to show as little papillæ on the skin surface on the fifth or sixth day of incubation; that the insinking of the proximal end of the down begins about the twelfth day of incubation; and that no shaft rudiment makes its appearance until about the twenty-second day of incubation. New barb-vane ridges are developed in the epidermal wall opposite to the shaft rudiment, as growth continues, and the ridges next to the shaft rudiment become fused into it laterally. The first feather continues to grow until the bird is nearly full grown, when a second feather begins to develop in the same papilla at the base of the first feather. When the second feather begins to develop a quill is formed at the proximal end of the first feather, but the proximal end of the quill has not become cornified, so that a connection is established between the proximal end of the quill of the first feather and the distal end of the second feather (Figs. 90 to 96, Plate VII). The second feather thus pushes the first feather out of the socket upon its tip. The connection between the two feathers is soon broken and the first feather falls off.

The first feather of the duck is regarded as a stiff down feather. I have failed to find any writer who regards it as in any sense a definitive feather, or a feather of the second generation. The fact that it begins to appear upon the skin surface on the fifth or sixth day of incubation, the time when the first down of other birds begins to show, indicates that there has been no short-

ening of feather development, and therefore proves this first feather to be the first down. The fact that the shaft rudiment of the first definitive feather of the duck does not make its appearance until after the seventeenth day of incubation, but that it does appear before the duckling is hatched, and that the first feather continues to grow for many days after the hatching, prove that in the development of the first feather of the duck there are stages of development which are exactly paralleled during the development of the down and first definitive feather of other birds. These stages may be briefly summarized for the sake of comparison.

From the fifth or sixth day of incubation to about the twelfth day of incubation the first feather is a slender outgrowth of the epidermis with a dermal core. From the twelfth to the seventeenth day an invagination at the proximal end of the first feather occurs and a feather pocket is formed. On or about the eighteenth day that portion of the feather which lies within the skin surface begins to enlarge. About the twenty-third day the shaft rudiment is formed by the coalescing of two barb-vane ridges. From this time onward barb-vane ridges are becoming merged into the shaft rudiment and new barb-vane ridges are being developed in the epidermal wall of the feather opposite to the shaft rudiment. At the limit of growth of the feather, barb-vane ridges cease to develop and a quill is formed by a process fully described by Davies for the definitive feather (p. 597, *et seq.*).

These stages of development and growth cover the whole period of the development and growth of the first down and the first definitive feather of most birds, but of only the first feather of the duck. The first feather of the duck is therefore a combination of the first down and the first definitive feather of other birds, and undoubtedly represents the primitive relation between these two structures. The first down is morphologically the distal end of the first definitive feather. This relation is very marked in Figure 58, Plate V, in Figures 70 and 71, Plate VI, and in Figures 97 and 101, Plate VII. Figure 85, Plate VI, represents a condition found where a plumulaceous definitive feather follows a first down. Except for the distinct growth mark where barbules are lacking, there is scarcely a difference in structure between the barb-vanes of the two parts of this feather. In a pennaceous feather the barbs and barbules are shorter and stiffer. Most definitive feathers are partly pennaceous and partly plumulaceous, so that in a single feather are combined the rigidity of the pennaceous definitive feather and the soft fluffiness of down.

Davies makes the statement that in the course of development of the down the pulp tissue pushes in between the barb-vane ridges and finally comes to surround the ridges almost completely, only a thin layer of cells serving to attach the ridge to the feather sheath as the peritoneum attaches the digestive tube to the body wall (p. 581). Only one of his figures (7) partially supports this statement, and it is diagrammatic. Strong did not find such a condition in the definitive feather, and I have failed to find it at any stage in the development of the first down. I have prepared Figures 47 to 51, Plate IV, to illustrate the conditions at the distal

end of a first down of a fourteen-day chick embryo (47 to 50 and 1, Figure 1, Plate I).

Figure 47 represents two barb-vane ridges in cross section distal to where the most distal barbules become attached to the barb. These two barb-vane ridges show a decided reduction in the number of barbule cells (bbl. cl) all of which are large. The cylinder cell layer (cl. cyl) has begun to separate the barb vane ridge from the sheath cells. The axial plate (ax. pl) is represented by large, irregular cells. There is a well developed basal membrane (mb. ba) which confines the dermal pulp to the center of the feather rudiment. In Figure 48 the barbule cells remain the same in number, but all of them are cut nearer their distal ends, and are therefore smaller. The cylinder cell layer more nearly separates the barb-vane ridge from the sheath cells. In Figure 49 barbule cells have disappeared, but the barb rudiment persists as a row of cells within the complete sheath of cylinder cells; in the center four cells represent the medulla of the barb. Residual cells occur between the ridges, and a basal membrane still shuts the pulp away from the barb-vane ridges and the spaces between them. In Figure 50 nine barb-vane ridges are cut across at different distances from their distal ends. They are in reality rings of cylinder cells enclosing cells which are destined to form the extreme distal ends of the down barbs. Residual cells fill the spaces between the barb-vane ridges, and a basal membrane confines the dermal pulp to the central region of the feather. In Figure 51 the feather rudiment is reduced to the feather sheath and central pulp separated by a series of residual cells. Barb-vane ridges have entirely disappeared.

VI. SUMMARY.

1. The development of the barbs and barbules is similar in the first down and the definitive feather.

2. The barbule cells of the down never develop hooked barbicels, but some of the distal cells may give off filamentous barbicels from their distal end. These filamentous barbicels are homologous with the barbicels which are developed from the definitive feather barbule cells.

3. The first down has no shaft. The barb-vanes which compose the first down are continuous and separate through the entire length of the down.

4. The first down has no quill. The down barb-vanes pass without interruption into the first definitive feather barb-vanes, either as entirely separate barb-vanes or else as a more or less homogeneous horny cylinder which can be split along lines continuous with the barb-vanes by pressing or rubbing the so-called "quill" between two hard surfaces. The horny cylindrical connection between the down and the first definitive feather is frequent among birds whose period of incubation is less than seventeen days.

5. No shaft is formed at the extreme distal end of the first definitive feather. The rudiments of a shaft begin to appear several millimeters proximal to the distal end of the feather by the coalescing of two or more barb-vane ridges.

6. The dermal pulp tissue is confined to the central region of the first down and does not separate the barb-vane ridges from each other nor from the layer of sheath cells at any stage of development. This is also true of the definitive feather.

7. The first down and its succceeding definitive feather are produced by one continuous growth, and therefore cannot be regarded as two distinct feathers. The first down is the plumulaceous tip of the first definitive feather.

8. Barbules are rarely entirely lacking in the first down. A typical down barbule is made up of a number of lengthened barbule cells placed end to end, the resulting barbule being long and slender, and not differing from the barbules of plumulaceous definitive feathers.

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EXPLANATION OF ABBREVIATIONS.

ax. pl. Axial plate.
bbl. Barbule.
bbl. cl. Barbule cell.
brb. Barb.
brb'. Down barb.
brb. crs. Barb ridge or vane.
brb. df. Definitive feather barb.
cl. cyl. Cylinder cell layer.
cl. im. Mucous intermediate cell layer.
cl. in. Intermediate cell.
cl. pig. Pigment cell.
cl. tu. Sheath cell layer.
cpl. sug. Red blood corpuscle.
ctx. Cortex.
drm'. Derma.
Drm. pp. Derma of papilla.
dst. Distal.
Ep. Epitrichial layer.
fil. Barbule cell filament.
grm. df. Definitive feather germ.
hr. Cornified tissue.
mb. ba. Basement membrane.
med. Medulla.
Mp. Malpighian layer.
nl. Nucleus.
nll. Nucleolus.
plp. Down pulp.
pp'. Down papilla.
prx. Proximal.
tu. ep. Epitrichial sheath.

PLATE I.

Figures 1, 6, 7, 8, 9, from the chick embryo. Figures 4 and 5, from embryo of Sterna hirundo. Figures 2 and 3, semidiagrammatic from feathers of Larus atricilla.

Fig. 1. Longitudinal section of developing down and cross section of skin from 14-day embryo. x 28.

Fig. 2. Diagram showing the relation of the down to the first definitive feather when each down barb is continuous with one or more first definitive feather barbs.

Fig. 3. Diagram showing the relation of the down to the first definitive feather when a so-called quill occurs between them.

Fig. 4. Semidiagrammatic cross section of down. x 141.

Fig. 5. Semidiagrammatic cross section of a definitive feather. x 103.

Fig. 6. Portion of a down papilla from 8-day embryo, longitudinal section of the papilla. x 618.

Fig. 7. A portion of a cross section of down at 7 in Figure 1. x 618.

Fig. 8. A portion of a cross section of down at 8 in Figure 1. x 618.

Fig. 9. A portion of a cross section of down at 9 in Figure 1. x 618.

Figures 7, 8, and 9 represent three stages in the development of the down at the time when the insinking of the base begins.

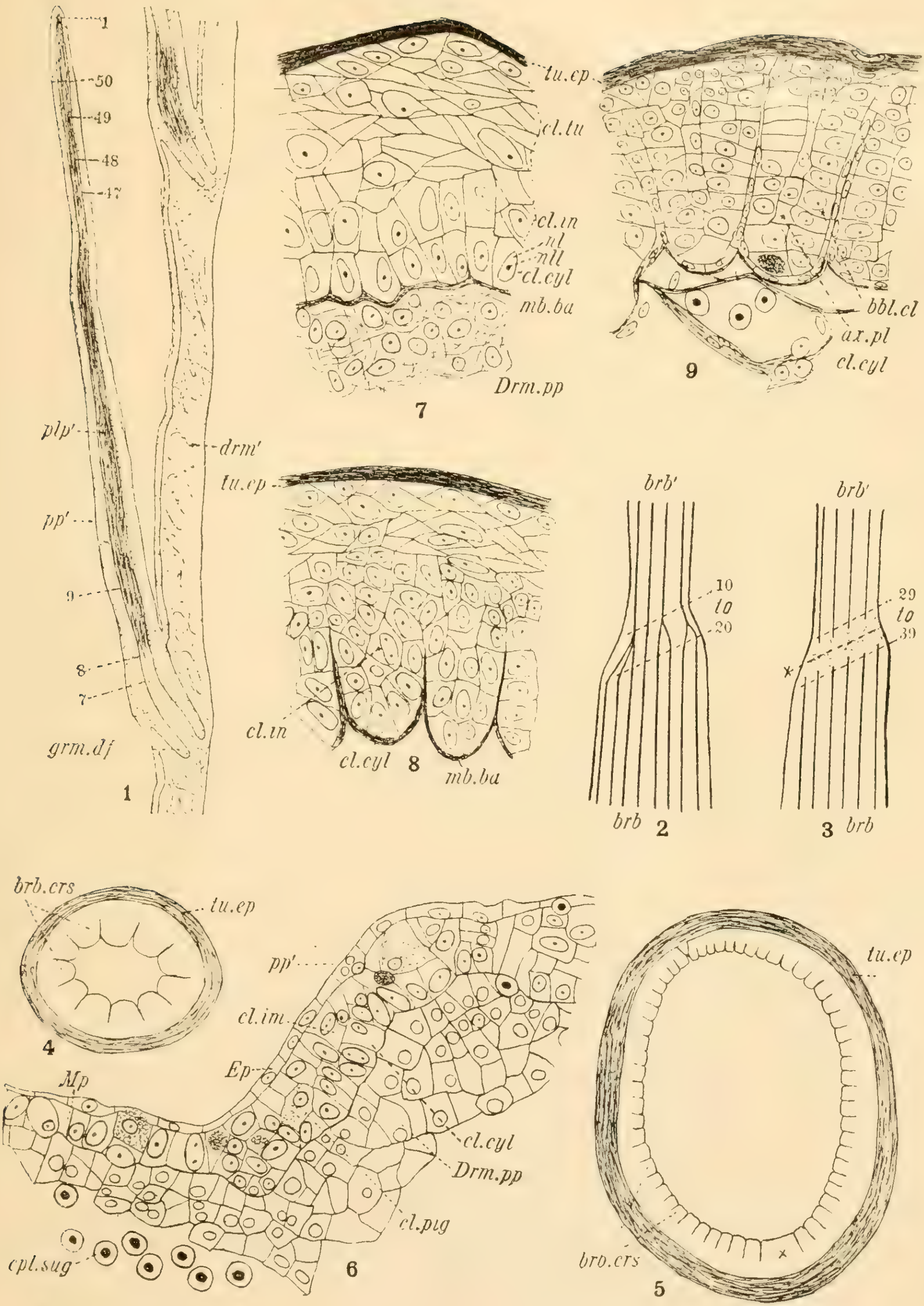
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PLATE II.

Figures 10 to 20 are from an 18-day chick embryo. Figures 21 to 28 are from a 21-day embryo ready to hatch.

Figs. 10 to 20. A series of cross sections of two barb vanes in the region of transition from the nestling down to the first definitive feather. At 10 to 20, Plate I, Figure 2. x 323.

Figs. 21 to 28. A series of cross sections of a single first down feather barb which was wholly cornified, to illustrate the passage of the first down barb into two first definitive feather barbs. x 618.

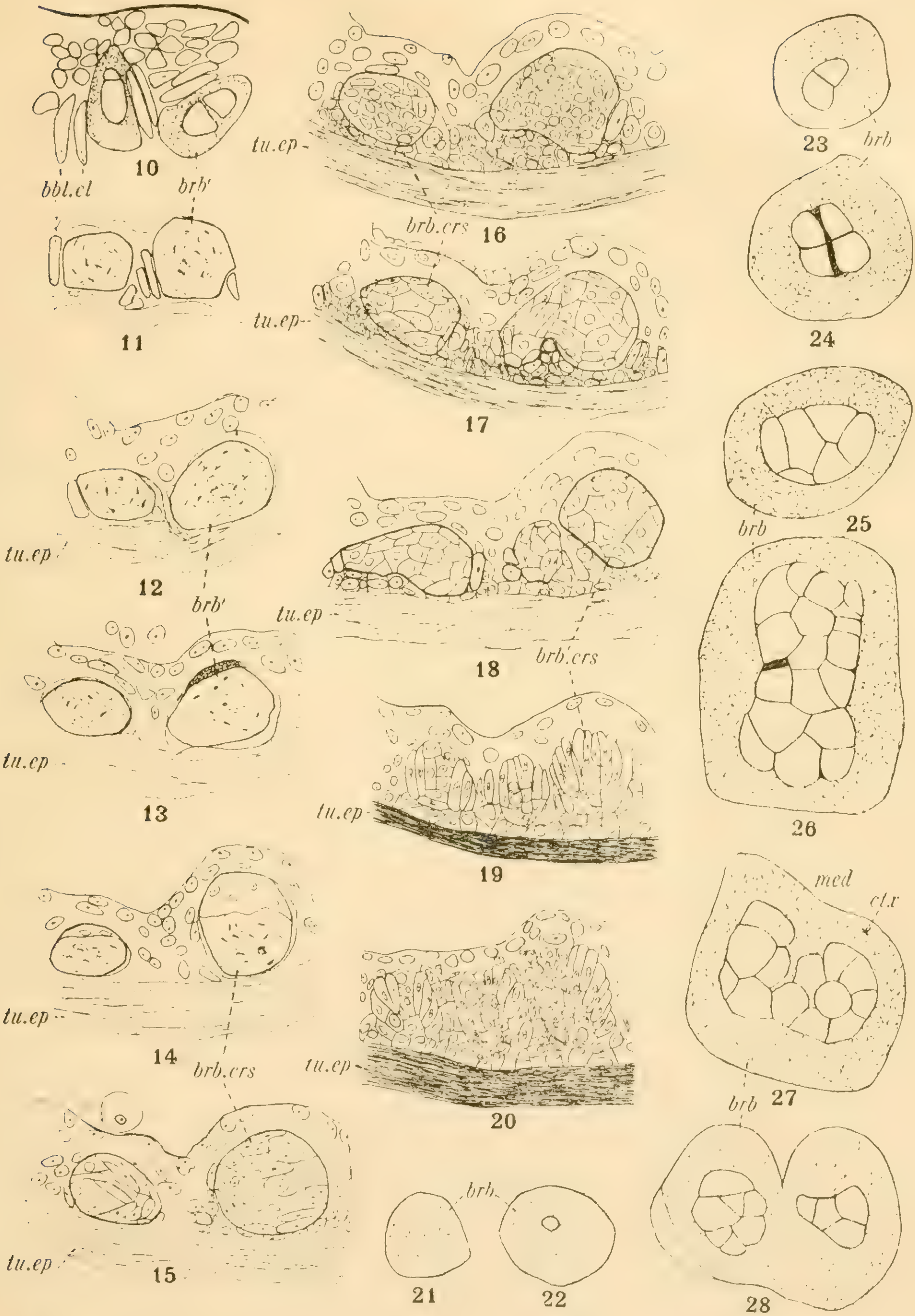
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PLATE III.

All figures are from a 20-day chick embryo.

Figs. 29 to 33. Entire cross sections of down. x 141. All cellular structure has disappeared.

Figs. 34 to 39. Cross sections of the feather, passing proximally into the distal end of the definitive feather. 34, 35, and 39. x 618. 36, 37, and 38. x 323.

Figures 29 to 39 form a series to illustrate the passage of the down into the definitive feather when a so-called "quill" is formed, that is, when the individual down barbs are lost in a horny ring, at Fig. 3, Plate I.

Figs. 40 to 44. Cross sections at X in Figure 2, Plate I, at different stages in the development of this region, to illustrate the reduced differentiation of the cells which results in a barb devoid of barbules. 40, 41, and 42. x 371. 43 and 44. x 516.

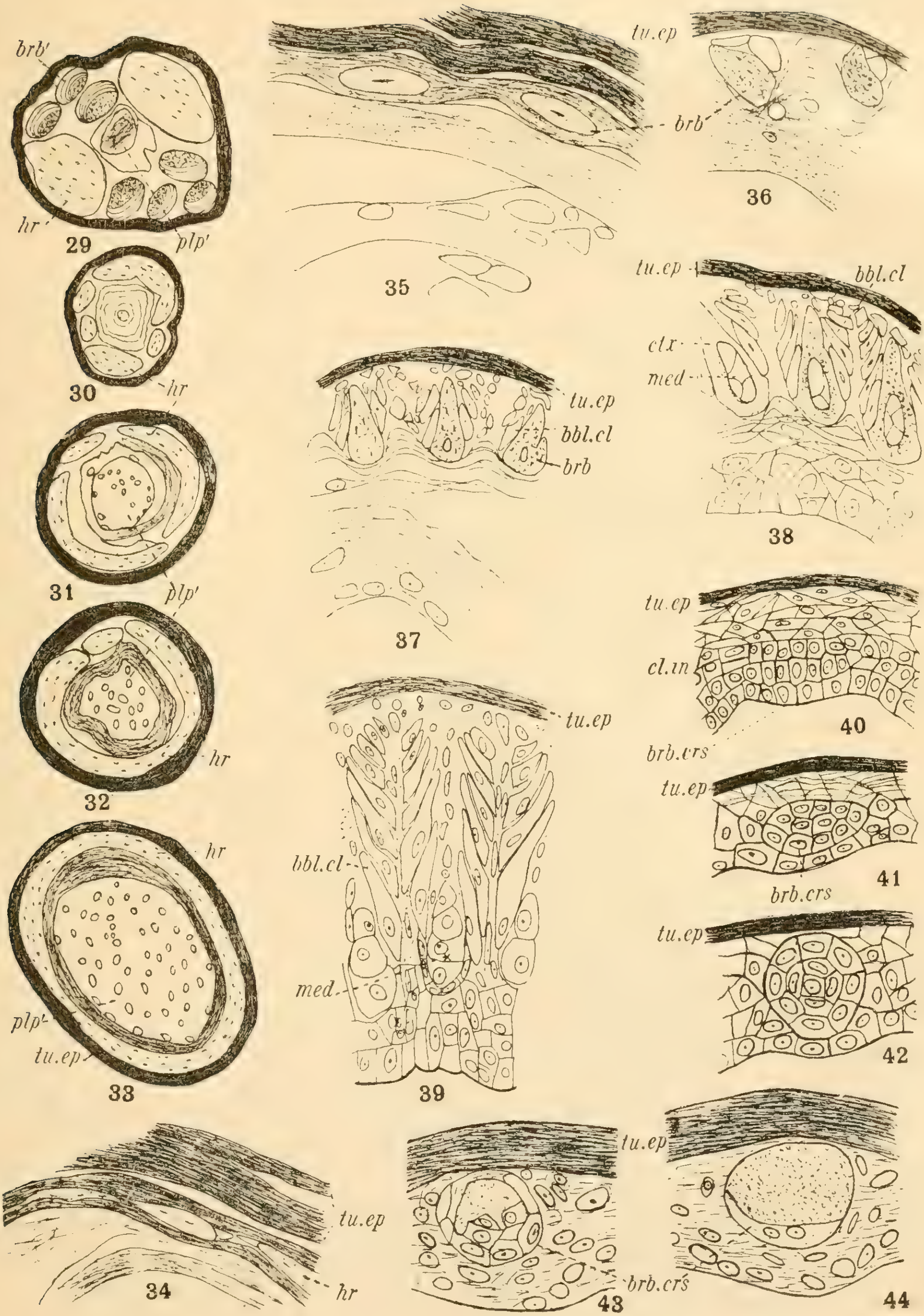
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PLATE IV.

Figs. 45 and 46. From a 20-day chick embryo. x 618. Taken in the region marked X, Figure 3, Plate I, at different stages in the development of this region.

Figs. 47, 48, 49. Cross sections of barb-vane ridges at 47, 48, 49, Figure 1, Plate I. x 618.

Figs. 50 and 51. Entire cross sections at 50 and 1, Figure 1, Plate I. x 618.

Fig. 52. A completely cornified down barbule from Larus atricilla. x 330.

Fig. 53. Distal ⅖ of a down barb with barbules, from Larus atricilla. x 28.

Fig. 54. A barbule with filaments (fil), one of which is a hooklet or hamule, at 54, Figure 142.

Fig. 55. A barbule with filaments (fil) at 55, Figure 142.

Fig. 139. A down barb dividing into two definitive feather barbs, one definitive feather barb having broken away. From a fully fledged Crymophilus fulicarius. x 62.

Fig. 140. Four down barbs passing into definitive feather barbs, showing incomplete separation of the barbs. From a fully fledged Oxyechus vocifera. x 28.

Fig. 141. A single down barb passing into three definitive feather barbs. From a fully fledged Actitis macularia. x 28.

Fig. 142. A single down barb dividing into three definitive feather barbs. Barbules are fully developed along the whole course of this feather. From a fully fledged juvenile Larus atricilla. x 39.

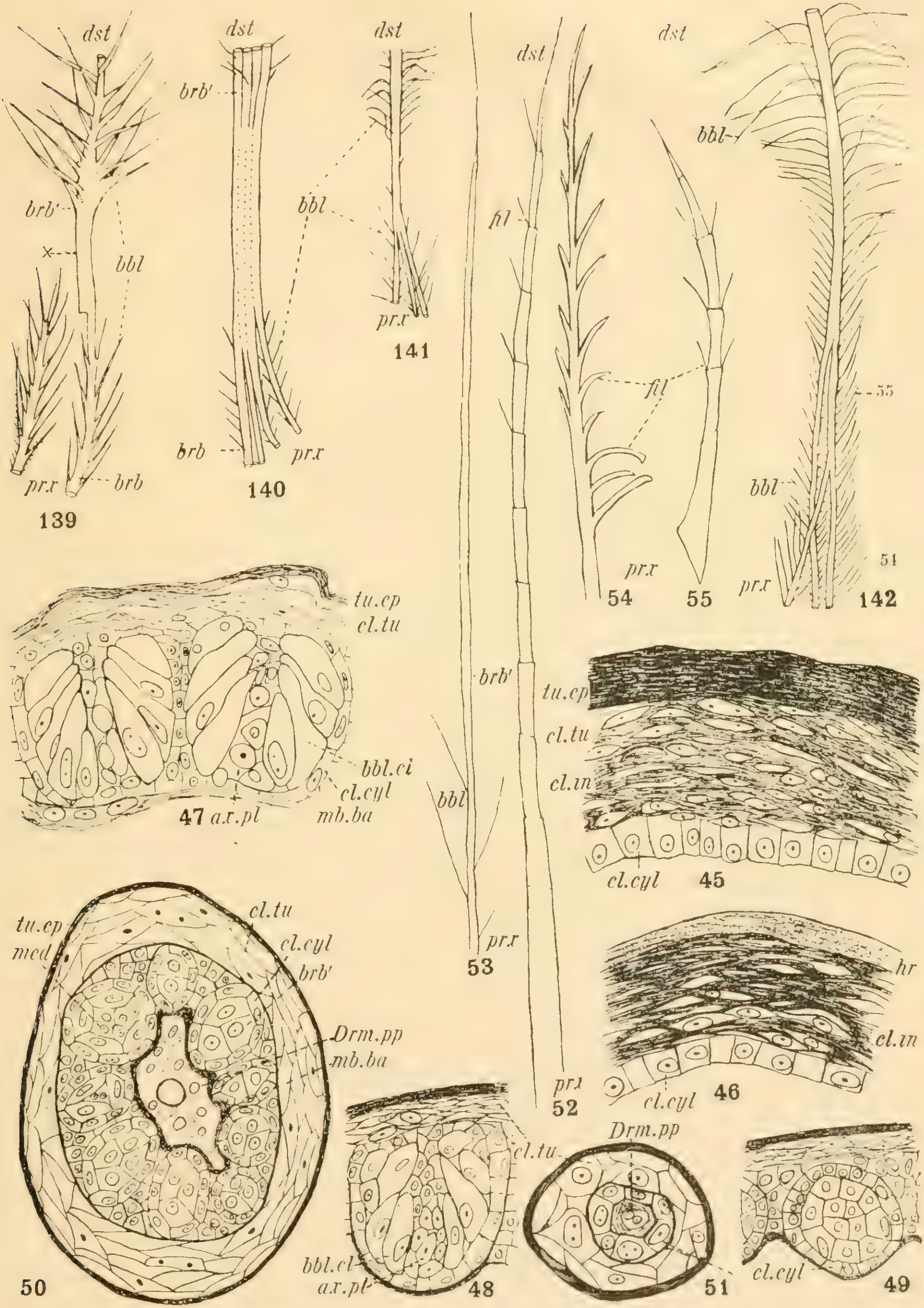
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PLATE V.

All figures are photographs of definitive feathers with down attached. x 1½.

Figs. 56 and 57. American Woodcock (*Philohela minor*).
Fig. 58. Killdeer (*Oxyechus vocifera*).
Figs. 59, 60, and 61. Spotted Sandpiper (*Actitis macularia*).
Fig. 62. Laughing Gull (*Larus atricilla*).
Fig. 63. American Osprey (*Pandion haliætus carolinensis*).
Fig. 64. Red-billed Tropic Bird (*Phæthon æthereus*).
Figs. 65 and 66. Cormorant sp? (*Phalacrocorax sp?*).
Figs. 67 and 68. Bob-white (*Colinus virginianus*).
Fig. 69. Chick (*Gallus*).


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PLATE VI.

All figures are direct prints of definitive feathers with down attached. x 1.
Fig. 70. Holbœll Grebe (*Colymbus holbœllii*).
Fig. 71. Least Grebe (*Colymbus dominicus brachypterus*).
Fig. 72. Pied-billed Grebe (*Podilymbus podiceps*).
Fig. 73. Loon (*Gavia imber*).
Fig. 74. Whiskered Auklet (*Simorhynchus pygmæa*).
Fig. 75. Dovekie (*Alle alle*).
Fig. 76. Herring Gull (*Larus argentatus*).
Fig. 77. Laughing Gull (*Larus atricilla*).
Fig. 78. Common Tern (*Sterna hirundo*).
Fig. 79. Roseate Tern (*Sterna dougalli*).
Fig. 80. Least Tern (*Sterna antillarum*).
Fig. 81. Black Tern (*Hydrochelidon nigra surinamensis*).
Fig. 82. Sooty Tern (*Sterna fuliginosa*).
Fig. 83. Anhinga (*Anhinga anhinga*).
Fig. 84. Man-o'-War Bird (*Fregata aquila*).
Fig. 85. Audubon Shearwater (*Puffinus auduboni*).
Fig. 86. Booby sp? (*Sula sp?*).
Fig. 87. Red-billed Tropic Bird (*Phaethon ætherus*).
Fig. 88. Leach Petrel (*Oceonodromas leucorhoa*)
Fig. 89. Blue-faced Booby (*Sula nebauxii*).

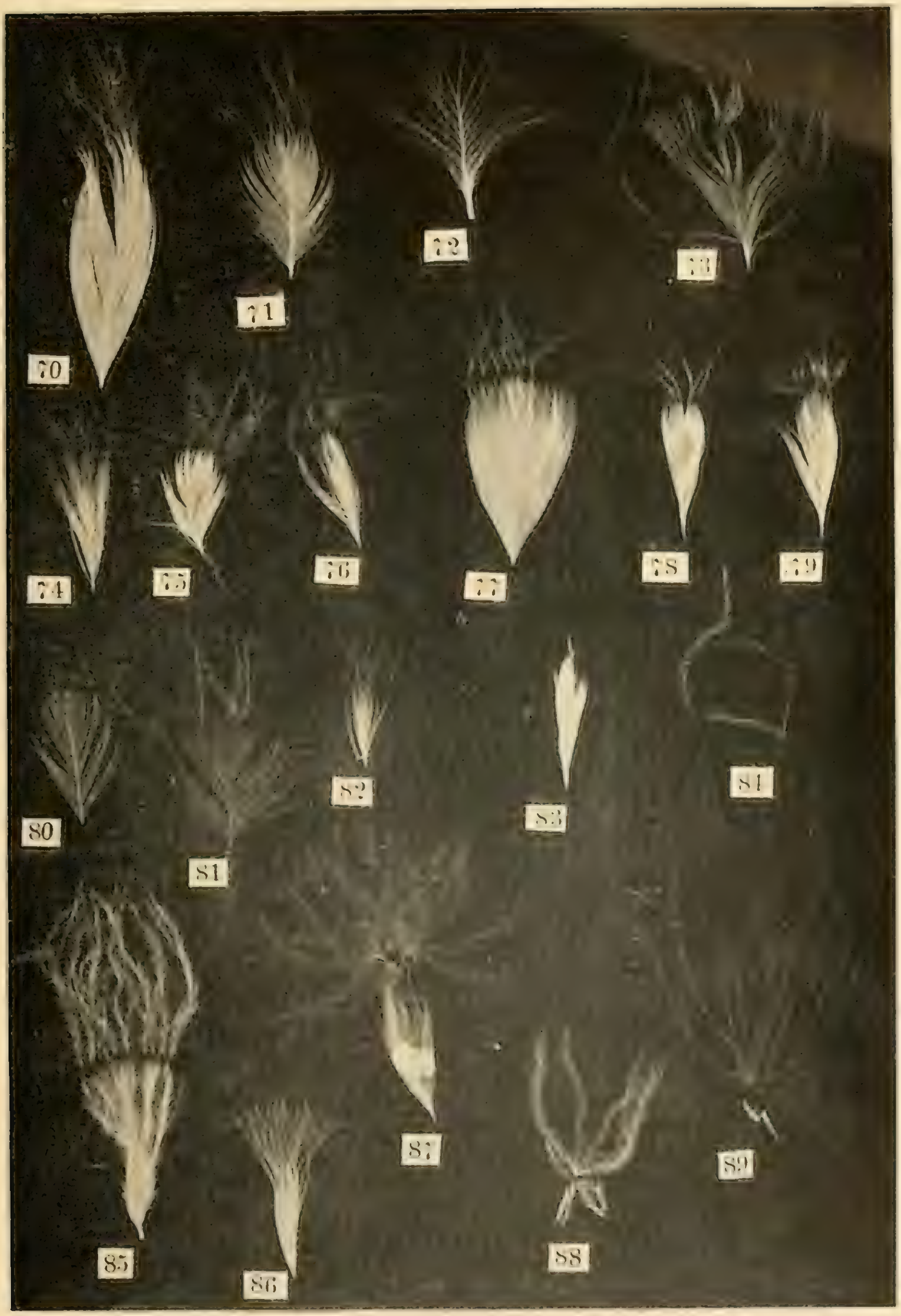
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PLATE VII.

All figures are from direct prints of definitve feathers with down attached to their tips. x 1.

Figs. 90 and 91. American Merganser (*Merganser americanus*).
Fig. 92. Ruddy Duck (*Erismatura jamaicensis*).
Fig. 93. Mexican Duck (*Anas diazi*).
Fig. 94. Pintail (*Dafila acuta*).
Fig. 95. American Golden-eye (*Clangula clangula americana*).
Fig. 96. Canada Goose (*Branta canadensis*).
Fig. 97. American Flamingo (*Phœnicopterus ruber*).
Fig. 98. White Ibis (*Guara alba*).
Fig. 99. American Bittern (*Botaurus lentiginosus*).
Fig. 100. Florida Gallinule (*Gallinula galeata*).
Fig. 101. Virginia Rail (*Rallus virginianus*).
Fig. 102. American Coot (*Fulica americana*).
Fig. 103. American Avocet (*Recurvirostra americana*).
Fig. 104. Red Phalarope (*Crymophilus fulicarius*).
Fig. 105. Northern Phalarope (*Phalaropus lobatus*).
Fig. 106. American Woodcock (*Philohela minor*).
Fig. 107. Wilson's Snipe (*Gallinago delicata*).
Fig. 108. Pribilof Sandpiper (*Arquatella ptilocnemis*).
Fig. 109. Western Solitary Sandpiper (*Helodromas solitarius cinnamomeus*).
Fig. 110. Yellow-legs (*Totanus flavipes*).
Fig. 111. Western Sandpiper (*Ereunetes occidentalis*).
Fig. 112. Mountain Plover (*Podasocys montanus*).
Fig. 113. Semipalmated Plover (*Ægialitis semipalmata*).
Fig. 114. Domestic Fowl (*Gallus domesticus*).
Fig. 115. Bob-white (*Colinus virginianus*).
Fig. 116. Red-tailed Hawk (*Buteo borealis*).
Fig. 117. American Osprey (*Pandion haliætus carolinensis*).
Fig. 118. Barred Owl (*Syrnium varium*).


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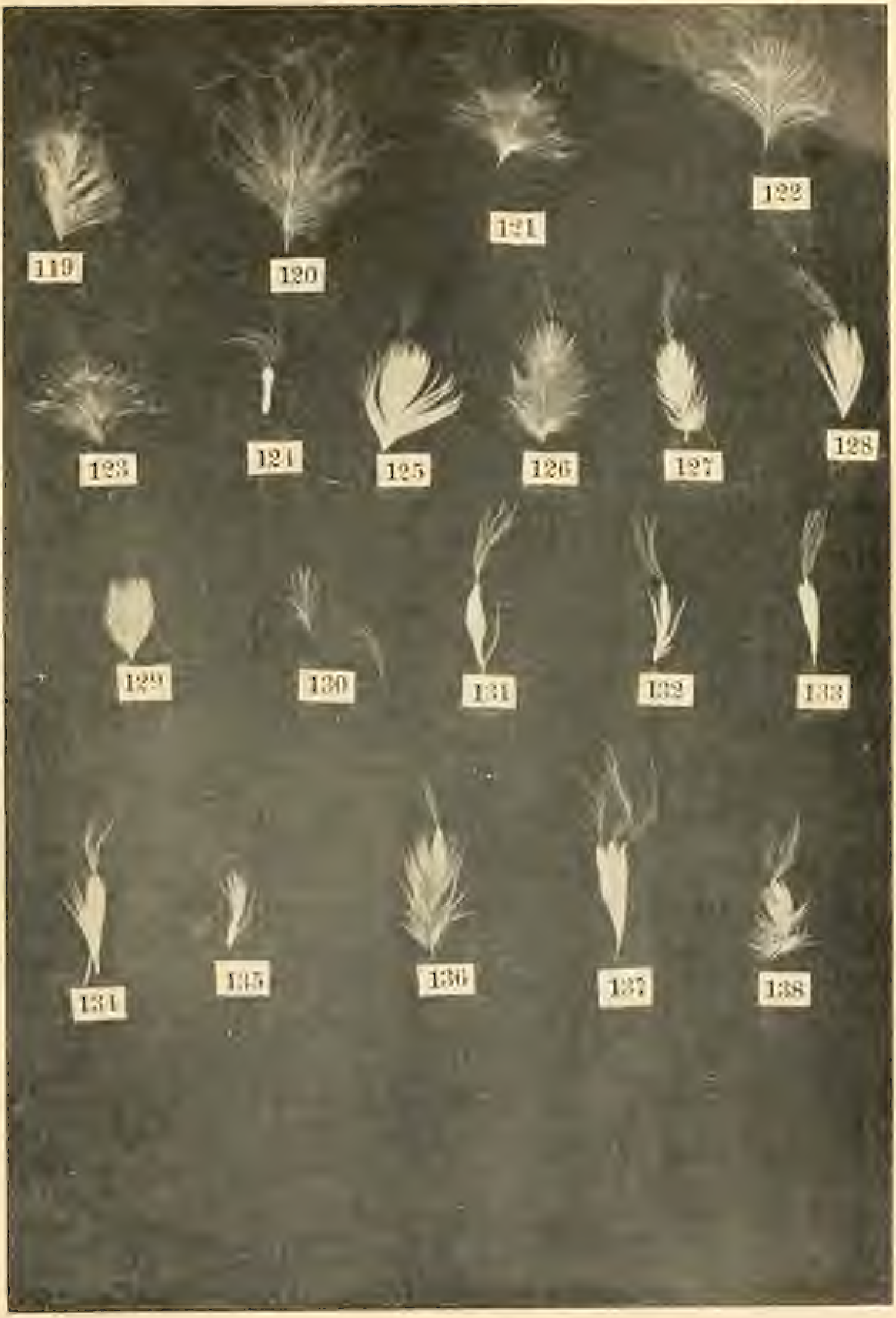
PLATE VIII.

All figures are from direct prints of definitive feathers with down attached to their tips. x 1.

Fig. 119. Screech Owl (*Megascops asio*).
Fig. 120. Great Horned Owl (*Asio virginianus*).
Fig. 121. Nighthawk (*Chordeiles virginianus*).
Fig. 122. Whippoorwill (*Antrostomus vociferus*).
Fig. 123. Nuttall's Poorwill (*Phalænoptilus nuttallii*).
Fig. 124. American Crow (*Corvus brachyrhinchos*).
Fig. 125. Cowbird (*Molothrus ater*).
Fig. 126. Baltimore Oriole (*Icterus galbula*).
Fig. 127. Meadowlark (*Sturnella magna*).
Fig. 128. Red-winged Blackbird (*Agelaius phœniceus*).
Fig. 129. Red-eyed Vireo (*Vireo olivaceus*).
Fig. 130. Blue Jay (*Cyanocitta cristata*).
Fig. 131. Bobolink (*Dolichonyx oryzivorus*).
Fig. 132. Red-headed Woodpecker (*Melanerpes erythrocephalus*).
Fig. 133. Red-headed Blackbird (*Agelaius phœniceus*).
Fig. 134. Catbird (*Galeoscoptes carolinensis*).
Fig. 135. Song Sparrow (*Melospiza cinerea melodia*).
Fig. 136. Cowbird (*Molothrus ater*).
Fig. 137. Green Heron (*Butorides virescens*).
Fig. 138. American Robin (*Merula migratoria*).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